2

The Behavior of the Red-winged Tinamou, *Rhynchotus rufescens*

(Figures 1-5, Table 1)

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An ethological study was done on captive red-winged tinamous, *Rhynchotus rufescens*. Descriptions of their behavioral repertoire are given, including maintenance, locomotory, feeding, agonistic, vocal, and reproductive behavior. Some qualification and comparison of behavior with other species of tinamous are made.

Introduction

The red-winged tinamou is one of approximately 45 species of tinamous which comprise the monofamilial avian order, Tinamiformes (Meyer de Schauensee, 1966). The family, Tinamidae, is neotropical. All the species, however, are found in South America, and only five have discontinuous distributions into Central America with four of these extending as far north as Mexico. Within this wide area, they are the dominant ground birds, filling most of the terrestrial habitats from Mexico, south to Tierra del Fuego. The tinamids are divided into nine distinct genera (Meyer de Schauensee, 1966). These are listed on Table 1 with the numbers of species, comparative size of the birds, habitats, and distributions.

They range in size from as little as a small quail to as large as a domestic chicken. Their coloring and behavior render them extremely cryptic and may explain why they have been so little studied. Usually males and females are similarly marked. In general appearance and behavior they may be imagined to resemble something between a rail and a gallinaceous bird.

Although equipped with a keeled sternum and capable of flight, their closest relatives are most probably among the ratites. The Rheiformes seem the most likely (Simpson, 1958), for they share such things as certain behavioral traits (sole male incubation and some displays), some structures (copulatory organs, aftershafted feathers, fine parts of the palate and rhampotheca; Parkes and Clark, Jr., 1966), and a not too dissimilar restricted distribution. Both tend to have a very reduced tail. They also share some egg shell characteristics (Tyler and Simkiss, 1959).

Clay (1957), however, did not find Mallophaga helpful in elucidating the relationship between these two groups. Jehl (1971) could find nothing in the comparative plumage patterns of chicks that would indicate an affinity with any of the ratites, while Sibley and Frelin (1972), on the basis of egg-white proteins, would place tinamous near the kiwis.

As with much of the world's fauna, these birds are facing a double assault on their existence by man's ever increasing population. Their eggs and flesh are eaten by man. The meat in particular is considered a delicacy. But most important is the destruction of habitats which denies these birds a place in which to live. Many of these forms are headed for extinction in the not too distant future.

Shy and secretive, tinamous are reluctant fliers, preferring to run and hide when disturbed. A few species have been reported to perch or roost in trees (Skutch, 1959; and Wetmore, 1965) or to fly spontaneously without being hard pressed (Pearson and Pearson, 1955; and Lancaster, 1964). Tinamous tend to be omnivorous, eating seeds, fruits, insects, other invertebrates, and small vertebrates.

Table 1. Summary of the Family, Tinamidae, by Genera

Genera	Number of Species	Size of Birds	Habitat	Distribution
1. *Tinamus*	5	Large	Tropical and subtropical forests	Southern Mexico, Central America, northern and central South America
2. *Nothocercus*	3	Medium	Tropical and subtropical forests	Central America, northwestern South America
3. *Crypturellus*	20	Medium to small	Tropical and subtropical forests	Southern Mexico, Central America, central and northern South America
4. *Rhynchotus rufescens*	1	Large	Tall grasslands and pampas	Brazil, Bolivia, Paraguay, Uruguay, and Argentina
5. *Nothoprocta*	6-7	Medium	From semiarid thorn forests up to subalpine Puna	The Andes from Ecuador south to Chile and Argentina
6. *Nothura*	5	Small	Short grasslands	Southern South America
7. *Taoniscus nanus*	1	Very small	Secondary forest-savannah	Sao Paulo State of Brazil
8. *Eudromia*	2	Large	Arid regions	Southern South America
9. *Tinamotis*	2	Large	From temperate Puna up to alpine regions	Southern Andes from southern Peru south to Chile and Argentina

A unique feature of tinamous is the nature of their eggs which have a very glossy, mirrored surface. Although tinamous are ground nesters, the eggs are one solid color without the protective camouflage that one might expect. Even the colors seem maladaptive as, depending on the species, they are pastel pink, blue, pea green, or various shades of violet or brownish-purples. The function and evolutionary significance of the gloss and colors is unknown but its maintenance has required some behavioral adaptations.

For those species which have been studied, it is usual for more than one female to contribute to a single clutch of eggs which is solely incubated by the male. The young are precocial and remain for a time with the attentive male.

Methods, Animals, and Facility

The purpose of this investigation was to describe the behavioral repertory of the red-winged tinamou and also to obtain some comparative data from the other tinamid species present.

I have observed the following species of tinamous in captivity:

Crypturellus obsoletus	Brown tinamou
Crypturellus noctivagus	Yellow-legged tinamou
Rhynchotus rufescens	Red-winged tinamou
Nothoprocta ornata	Ornate tinamou
Nothoprocta perdicaria	Chilean tinamou
Nothoprocta pentlandii	Andean tinamou
Nothura darwinii (one specimen)	Darwin's nothura
Nothura maculosa	Spotted nothura
Eudromia elegans	Elegant crested tinamou

Of the over 200 observational hours for this study, most were spent on six individuals of *Rhynchotus rufescens*, the red-winged tinamou. These birds were wild-caught, presumably as young in the state of Sao Paulo, Brazil. Individuals were marked with leg bands and were wing-tagged with colored nylon Saflag fabric fastened around the humerus.

The aviary was a 6.4 x 30.5 m greenhouse (Sheldrake, 1969) consisting of a wooden frame covered with plastic. It was heated with two thermostatically controlled, forced-air gas heaters, one at each end. Ventilation was accomplished by a thermostat and a time controlled two-speed fan. This operated in such a way that for five minutes of every hour the fan was operated by the timer, regardless of the temperature. Anytime other than this, when the temperature inside the aviary rose above the thermostatic setting, the fan was again activated.

Fresh, incoming air was equally distributed throughout the aviary by means of a perforated plastic tube, five feet in circumference, that ran the length of the ceiling. This flexible tube remained closed until the negative pressure caused by the exhaust fan's operation inflated it with air from the outside. This arrangement functioned to prevent birds from being exposed directly to a draft, especially important during the cold winter temperatures.

Initially the red-winged tinamous had free run of the entire eviary with other species of tinamous. During the first winter the birds contracted a respiratory viral infection. While this was fatal to some species, most of the red-winged tinamous were only mildly affected, but a few required force feeding for a time. With one indicated exception, no data from sick individuals were used in this paper.

Rhynchotus rufescens spent the first summer in an outdoor pen. They were then given their own enclosure within the aviary. The floor plan and dimensions are shown in figure 1.

Rye grass seed was sown over a portion of the aviary. Passion flower vines (*Passiflora* species) grew along and up the walls. Some locally wild grasses such as timothy were transplanted for additional cover, as well as clovers, mustard, etc. The probing and grazing behavior of these animals required a regular program of planting and transplanting to keep green areas. To simulate tall grass clumps, long dried grass stems and dried forbs were gathered and tied into bundles with a stake in the middle. These "artificial grass clumps" were placed along the walls and in line-of-sight rows which converged on my observation station. They gave the birds a sense of cover without obscuring them from view. In addition, to further break up the visual field of the birds which could see each other most of the time, low cardboard and burlap baffles that were also laid out in line-of-sight orientation were erected. When the birds could no longer see each other, there was marked increase in their vocalizations.

Most of the data on the red-winged tinamou were collected after the birds had been in captivity for about 18 months, five of which they had spent in their own enclosure.

Tinamous are very difficult to observe in the wild. Observations in the field are short term, chance sightings, or perhaps the result of luring birds briefly out from cover with an imitation of their call (Lancaster, 1964a). Lancaster (1964a) was able to determine the direction of movement of a calling male and put himself in its path in order to observe it as it passed. Continuous observations would be very rare with most species. Pearson and Pearson (1955) had some success in open, short grass grazing areas in Peru with *Nothoprocta ornata*, and Schäfer (1954) succeeded with *Nothocercus bonapartei* when the birds accepted him as a part of the habitat. Other investigators in the field were not so fortunate (Lancaster, 1964a, 1964b, and Beebe, 1925).

In 1892, Hudson described the habitat of *Rhynchotus rufescens* as being largely dominated by only a few coarse grass species, 1 to 2.5 m in height and growing in large tussocks. The most notable of these are *Cortaderia* (= *Gynerius*) species. More recently, Bump and Bohl (1965) state that tall (40 to 90 cm) clump grass is a favorite cover for these birds. It is these grass tussocks that structure the environment and the behavior of the red-winged tinamou. Alterations of the habitat to facilitate observations would probably render it unsuitable for the birds. Hudson (1920) reported that wherever the shorter European varieties of grass were planted, the red-winged tinamou disappeared. A field study of this species, then, would probably require many hours spent for very little behavioral data. Complete sequences of behavior might never be seen, and manipulations of the birds or the environment would be difficult or impossible. Wetmore (1926) mentions *Rhynchotus rufescens* as being difficult to see and collect in areas where they were common.

Aviary studies do have shortcomings, such as the possibility of disease and the chance that the unnatural environment will cause unnatural behaviors. One can obtain an accurate picture of most if not all of the behavioral repertoire of many birds from captive studies, if he has an understanding of their habitat and general behavior. There may be some behaviors which will not take place in an aviary due to the lack of proper stimuli, such as the reaction to certain predators, and there may be some behaviors caused in captivity due to stimuli not found in the wild (Kaufmann and Kaufmann, 1963). The latter sometimes are of interest in understanding the evolution of behavior. Work both in the field and in the aviary are important and the discrepancies between the two are of heuristic value. The captive data which predictably vary the most from field observations are those of frequencies of behavior, while descriptions of species-specific behavioral patterns should be very similar. This paper is mainly concerned with these behavioral

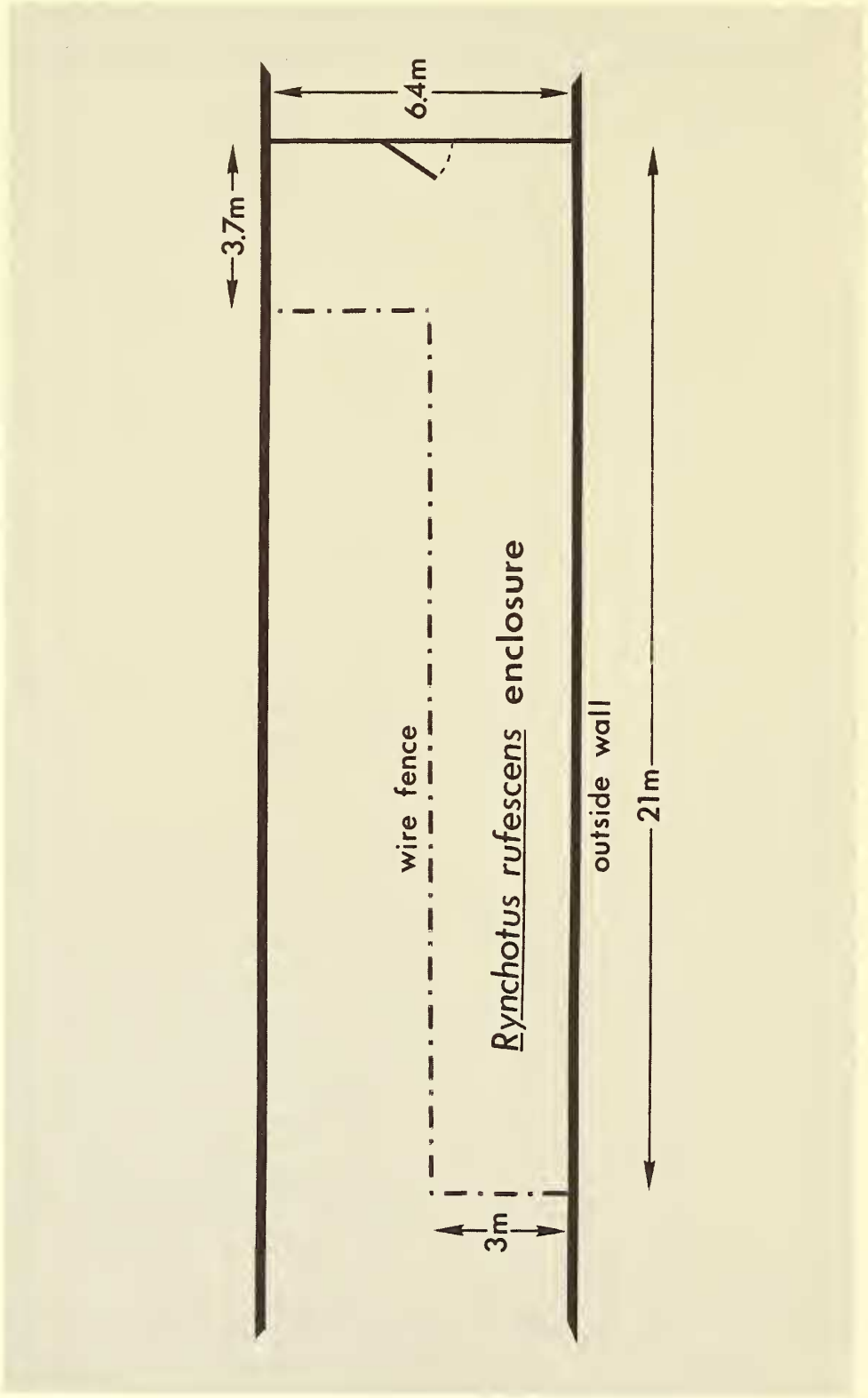

FIGURE 1. Floor plan of the *Rhynchotus rufescens* aviary.

patterns. In many cases of this kind, it is more efficient to have the aviary study precede the field work because familiarity with a species as to how it hides, its vocalizations, signs of feeding, droppings, etc., aid in locating it in the field and the recognition of incomplete behavioral sequences maximizes the data collected.

The shortcomings of the aviary can be made to work in one's favor. Assuming that behavior has changed only quantitatively and not qualitatively in captivity, behaviors rare in the wild may be repeated over and over by caged birds. This allows very careful recording of the behavior and sometimes the determination of what is causing it to happen so often. By manipulation one may reveal something of the drive(s) controlling this particular event. Also the birds may be bred out of season by light stimulation. Photography and other means of recording behavior are more easily accomplished in captivity since one knows where, within limits, it will occur and can in some cases increase the probability of its occurrence. Caution should be used in predicting what goes on, and how, in the wild based solely on captive studies (Kaufmann and Kaufmann, 1963).

Description

Rhynchotus rufescens is tan, brown, tawny, and black in a cryptic, barred pattern (see figure 2). This, combined with the animal's preference for sitting beside and partly under the overhang of a clump of grass, makes it extremely hard to see. The rufous of the primaries and initial secondaries is seen only when the wings are extended. Adults weigh about one kilogram, with the females tending to outweigh the males. Otherwise the sexes are identical. Positive sex identification by cloacal examination was attempted without much success in the red-winged tinamou, but was useful in other species (Bump and Bohl, 1965; and Bump and Bump, 1969). The sex of the individual *Rhynchotus rufescens* was determined behaviorally.

Considerable variation has been reported in the color of these birds from different geographic locations (Wetmore, 1926; Laubmann, 1930; and Naumburg, 1930). The birds from the state of Sao Paulo, Brazil, are darker than specimens from the north or farther south. Laubmann (1930) states that the birds farther south take on a more grayish cast. This probably reflects areas in which the climate is drier and the grayer tone of the plumage is adaptive. The birds used in this study came from southeastern Brazil and showed considerable variation in coloring. These specimens are now at the Laboratory of Ornithology, Cornell University, Ithaca, New York.

Locomotion and Stationary Postures

Rhynchotus rufescens has strong legs with what appear to be small feet in comparison with other terrestrial birds of similar size. Its feet likely have become reduced as an adaptation for cursorial locomotion through dense vegetation.

Walking and running

As the bird walks the head is moved back and forth in a horizontal, anterior-posterior direction in a mid-sagittal plane, similar to many walking birds. Bangert (1960) studied the coordination of the head movements with foot movements in the domestic chicken. These head movements probably function in giving a bird a series of stable visual images (Daanje, 1950). In *Rhynchotus rufescens*, these head movements are always associated with walking and never occur without foot movements as they do in some other tinamous, *Nothura maculosa* and *Nothoprocta ornata*. This was noted in the latter species by Pearson and Pearson (1955) in the field and was observed in both species in the aviary. In these two, the head movements of locomotion have taken on some signal function, become typically exaggerated, and may occur even when the birds are standing. It was probably from this source that the bowing head movements of *Eudromia elegans* evolved. The birds which use these behaviors live in fairly open environments, and these movements may serve in species recognition or take the place of contact calls; and, as with most visual displays, it is used only when the birds are out in the open.

The erect walking gait of the red-winged tinamou varies from slow steps to a rapid walk. When the bird runs, the head is held low with the neck outstretched almost horizontally. The back and forth head component disappears as the bird typically plunges through the grass. A run usually culminates in a fast turn with the bird immediately sitting behind a clump of grass and under its overhang.

Jumping

These birds jump with little effort and do so to get food, to escape from an aggressive encounter, or to attack another bird, but never to clear an obstacle. A jump may be taken backward, forward, or to the side. In order to jump, the bird must have its feet close together; it apparently cannot perform a running jump.

Several times I have seen a running bird trip over a dead branch or some other obstacle. I did not see the red-winged tinamou jump over the aviary's 45 to 60 cm high barriers. On the other hand, *Crypturellus noctivagus* usually walked around the 45 cm high barriers in its enclosure but when pressed easily hopped over. *Crypturellus* species are smaller than *Rhynchotus* and inhabit forests where solid barriers are commonly encountered.

Rhynchotus plunges into its environmental matrix rather than jumping or flying over it. It prefers to move on the level, and will walk

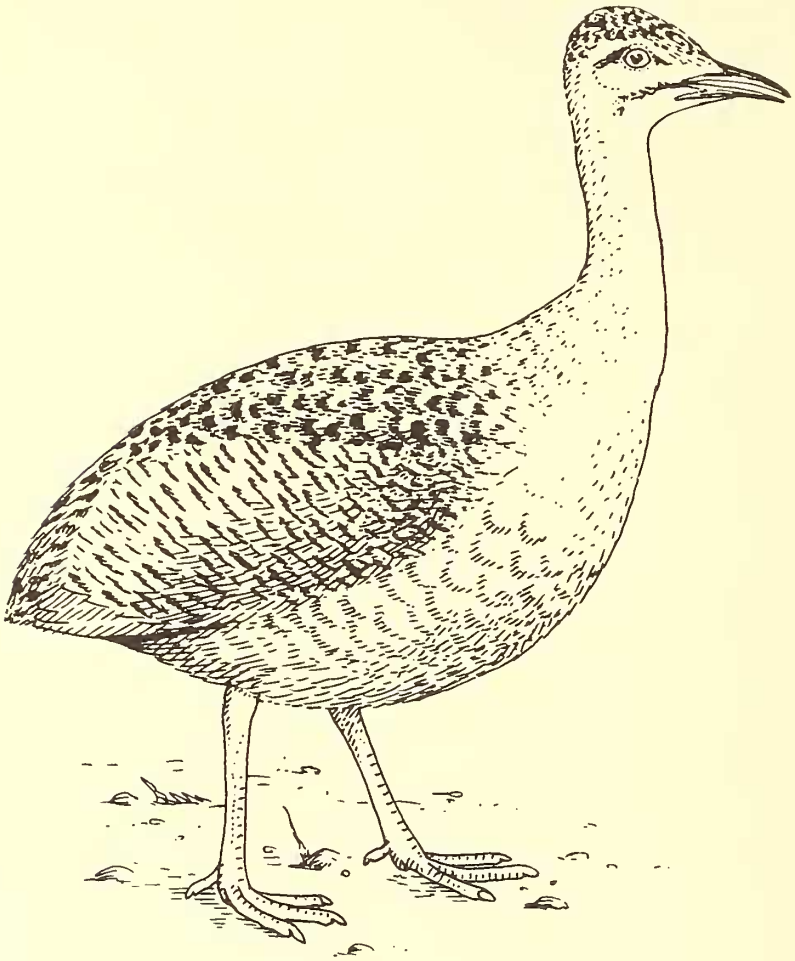

FIGURE 2. *Rhynchotus rufescens* adult.

around stones and other such obstructions.

Flying

When in a bare aviary, these birds take to wing at the slightest disturbance, but when provided with some ground cover, run for it.

Their wings are short and rounded much like those of the ruffed grouse, *Bonasa umbellus*. Their flight is noisy and accompanied by a high, shrill, pulsed whistle. When forced to flight they typically burst up unexpectedly at your feet with fast, continuous wingbeats. The wings make a rattling sound and the whole effect is well described by Hudson (1872) as similar "to the rattling of a light vehicle driven at great speed over a hard road." Even when I have seen a bird sitting on the ground and have been fairly certain that it would fly as I approached, it was still startling when the bird burst up from the ground. I am sure it would have a similar effect on a predator. Hudson (1920) reports that the birds can make only two or three flights in succession before they are too exhausted to fly or to run very far.

Alert posture

The birds assume the alert posture when mildly disturbed, as by a strange sound. In this posture the feet are brought fairly close together, probably to gain added height. The neck is extended upward and the back is almost vertical. They can "freeze" in this position for several minutes or may turn their heads and look around.

They normally stand and walk with their heads about 30 cm off the ground but, in the alert posture, they can stretch to a height of at least 45 cm.

Nothura maculosa also has an alert posture when it is not extremely disturbed. *Crypturellus noctivagus* does not have a pronounced upright posture; for this forest bird it is probably more important to look around environmental clutter than to attempt to see over it. This species does perform an interesting display when slightly disturbed which I call wing-flicking. It was easy to elicit simply by whistling and a bout was usually started by a bird in the open. These birds carry their wings slightly drooped, and a wing-flick is accomplished by a quick folding of the primaries. This produces a soft rustling sound and birds in cover come out and look around. This behavior is both mimetic and synchronized. They are soon moving about nervously, wing-flicking in almost perfect unison.

Crouching and sitting

While feeding, resting, or preening, the red-winged tinamou will occasionally crouch. The weight of the body is on the heels and tarsi; the body orientation is nearly horizontal. In addition, there is a post-copulatory crouch and a full posture, mentioned later, in which the male's body is held in a more upright position.

While sitting, the bird's breast is on the ground with its feet and legs folded under; the neck is held in a tight "S" curve above the breast.

High stepping and creeping walk

A peculiar type of walking behavior is seen when a bird is leaving the nest. Individual birds differ with respect to the distance traveled by this method, varying from a few steps to 4 m. The differences did not correlate with the sex of the individual. While walking away from the nest, the body is about the same distance from the ground as in normal walking, perhaps a bit lower. The feet are raised unusually high as though the animal were stepping over some obstacles. I was reminded of the walking behavior of a cat in wet grass. The area around the nest was not cluttered; sometimes well packed hay and straw formed the substrate, other times it was only bare, dry earth. I call this behavior "high stepping." This gait is faster than average walking and the bird is always moving directly away from the nest in a fairly straight line.

High stepping may function to reduce noise around the nest and may signal other birds as to the nest's location. Other birds noticed a high stepping individual and would cease momentarily what they were doing.

Another type of locomotion termed the "creeping" walk was seen only a few times performed only by males. The body, head, and neck are held low to the ground as the bird moves along. I believe this is a submissive behavior of males to particularly dominant individuals and will be discussed under agonistic behavior.

Standing

Rhynchotus, *Crypturellus noctivagus*, and other tinamous (possibly all other tinamous) rarely stand with their feet side-by-side. This condition has been noted by Raikow (1968) in the rhea. I have seen *C. noctivagus* standing with one foot on top of the other.

Maintenance Behavior and Comfort Movements

Head and bill care

Rhynchotus spends a great amount of time digging in the ground with its bill, and dirt, mud, and other debris frequently stick to it and sometimes to the head feathers. Head shaking, a sharp flicking of the head and bill, is usually the first method used by the bird to remove it. If unsuccessful, the bird will bring its foot up and scratch the head or bill. The foot is never placed over the wing. For very sticky items, the bird resorts to bill wiping on the substrate. The mucous secreted by earthworms is frequently removed in this way. Another way is to peck into soft soil several times.

Stretching

There are three types of stretching behavior. In

one, the wings while remaining folded are raised over the back. In another, one wing is extended downward until the primaries touch the ground while the ipsilateral leg is extended posteriorly. And finally, both legs may be extended together until they are straight. This raises the rump of the bird, but the head and neck remain low and may be slightly extended anteriorly.

Ruffle-shake

In this behavior plumage is ruffled and the body shaken from side to side in a rolling motion. It is used to straighten the feathers after preening, dustbathing, being mounted by another bird, and other plumage-disturbing activity. A wet bird will shake off some of the water by this method. At times this behavior would seem to have aggressive implications when a bird which had not been preening or disheveled in any way would suddenly ruffle and shake.

Dustbathing

This behavior occurs only during sunny periods of spring and summer. It may start abruptly when the sun breaks out from behind clouds, and it is most apt to occur between the hours of 10 and 11 a.m. and between 2 and 3 p.m. The bird selects a bare area where the soil is dry and dusty. The site is out in the open, never shaded or near vegetation or aviary walls. While walking, or occasionally standing, a bird may make intention movements for dustbathing by lowering its body and pecking obliquely to the side at the ground. These pecks, averaging about four, may function to test the suitability of the soil for dustbathing. Even when the bird is moving, all pecks are directed very near the same spot. To accomplish this, the first peck is made with the neck outstretched, and each additional peck is oriented more to the side compensating for the forward motion. The last peck usually requires an apparent awkward bend in the neck. The bird may then straighten up and continue walking, or it may turn sharply and sit very near the area of investigative pecks. From this position the bird continues to peck at the soil in front of its breast and to either side. Then, without rising, the bird scrapes with alternate feet and makes a quarter to a third turn, and then begins another bout of pecking at the soil in front of its breast. This sequence may be repeated several times until the soil is worked up and the bird is settled in a dustbathing scrape, a depression 4 to 8 cm deep.

The length of time the bird spends in the pecking, scraping, and turning bouts seems to depend on the degree to which the soil is worked up, how fine the soil is, and whether a depression is present from previous dustbathing. A bird entering an old dust scrape, or one starting in an area of fine, loose soil, may only peck, scrape, and turn a few times. While in a new area where the soil may be more hard packed, it takes much longer.

Finally, the bill is jabbed into the loosened earth and flicked caudally and laterally so that dust, pebbles, and dirt clumps are sent flying over the bird's back. The feathers of the back and rump are raised slowly after a time. Dust is thrown alternately over the shoulders. As dustbathing progresses, one folded wing is raised in such a way that the ends of the primaries slide over high on the back as the bird turns slightly on the opposite side. Now dust is directed only to the side newly exposed. Later the other side of the body is usually afforded the same treatment after the bird has turned in the other direction. Upon righting itself in the dust scrape, material may be directed at the back again, and the dorsal surface may become completely covered with dust. Frequently, the bird rests in this position for several minutes. At any point in the dusting sequence, further bouts of pecking, scraping, and turning may occur.

Dustbathing is terminated by the bird's rising and taking a few steps from the dusting scrape and ruffle-shaking. The bird emerges from the resulting cloud of dust usually to ruffle-shake again a few steps later. On a few occasions, a bird leapt from its dusting scrape aggressively at another bird that had come too close.

Dustbathing is mimetic and other birds are drawn to the area to dustbathe. Not all birds that come to an active site dustbathe themselves. Some approach an actively dusting bird, sit behind and off to one side, apparently to benefit from the dust it throws. If a dust scrape is vacated, one of these satellite birds may enter it and begin active dustbathing.

The length of dustbathing bouts can vary from a couple of minutes to well over half-an-hour. Eliminating the many abortive starts (those lasting less than 30 seconds) gives an average of about 13 minutes.

Mounting and copulatory behavior were associated with dusting especially during the bird's reproductive period. This usually occurred when a male would approach a dustbathing female. An attempted mount would usually cause her to leave her scrape. Frequently when the female left her scrape, she would solicit for copulation within the vicinity of the dusting area.

A fresh dustbathing scrape is easily identified. It is a depression about 20 cm in diameter and 4 to 8 cm deep. Around the outside of this circular cup, there is usually a trough about 3 cm wide and 1 cm deep resulting from the action of the bill.

The factors controlling dustbathing seem to be temperature of the soil and the air, sunshine or artificial light and radiant heat, humidity, and the presence of Mallophaga. Dustbathing does not take place until temperatures on the ground are

above 74° F and most often around 81° F.

I could regulate the air temperatures to some degree by means of the heaters. The temperature of the ground could not be controlled and remained quite cold throughout the winter. I found I could increase the chances of dustbathing occurring in the very early spring, when dusting was rare, by increasing the air temperature to near 80° F. I did not attempt to raise the humidity, which during periods of frequent dustbathing is quite high. Further, when an infra-red lamp was installed in an enclosure containing *Eudromia elegans* and *Nothoprocta perdicaria* and *Nothoprocta pentlandii*, the area under the lamp was warm to the touch, and this same area became an active dustbathing site.

It is probable that the factors which cause or are most apt to bring on dustbathing are the same factors which cause Mallophaga to become active. Rothschild and Clay (1952) mention the sensitivity of Mallophaga to temperature. I have noticed while doing avian surgery that the first indication of a failure in an operation was when the Mallophaga changed their preference from the bird to me. Without exception, this was an indication that the bird had expired. I assume that the cue for this emigration was a slight differential in temperature (Bair, 1950).

The presence of Mallophaga on the tinamous was noted repeatedly. I agree with Rothschild and Clay (1952) that the function of dusting is primarily to remove ectoparasites. They report that Mallophaga have been found in dusting scrapes. Silicon dioxide powder can be used for the collection of ectoparasites by lightly dusting a bird's feathers with it. Observations I have made on a cinder path indicate that the path was far more attractive to wild birds and even small mammals for dustbathing than were two adjacent areas where the soil was dry, fine, and dusty. Attempts to collect Mallophaga with the dust from the cinder path were not fruitful, but this may have been done at a time when the birds had cleaned themselves of most of their ectoparasites.

Dustbathing in other species of tinamous seems to be mimetic also. It is common to see one dustbathing bird soon joined by another. *Eudromia elegans* and *Nothura maculosa* were seen dustbathing in groups of twos and threes. *Nothura maculosa* dusting behavior was markedly different from *Rhynchotus*. The dust was stirred up and into the feathers mostly by rapid foot scraping movements and not at all by the bill which was ineffective in this way. Unlike many other birds, such as the galliforms, for example, the tinamous do not use their wings to get dust into their plumage. Nor do they use their bills to pick up dusting material as do rheas. Lancaster (1964) describes dustbathing in *Nothoprocta cinerascens* which is quite similar to the red-wing.

The two forest forms, *Crypturellus obsoletus* and *Crypturellus noctivagus*, were never seen to dustbathe. No sign of a dusting scrape was ever seen in their pen.

Eudromia elegans does not always ruffle-shake after a dusting bout. Several times I have seen them walking with a layer of dust on their backs, and one incubating male was liberally covered with dust. This could render a bird and the nest more cryptic in their dry habitat during incubation. Upon examining a red-wing one morning before any dustbathing had occurred, I lifted the feathers of the rump and found the skin covered by a layer of dusty grit.

Waterbathing

Eudromia elegans and *Rhynchotus* bathe very rarely. Also, Lancaster (1964) observed bathing only once in his observations on *Nothoprocta cinerascens*. Perhaps waterbathing may be accomplished by walking through wet vegetation. These birds, it was noted, are active dustbathers.

Crypturellus noctivagus was the most active waterbather of the tinamous that I observed. It bathes in pools as well as in the spray from a hose nozzle simulating rain.

It slowly walks back and forth through the spray, shaking the head. The bird lowers its body and creeps, shakes its head, and eventually sits. It may get up, creep around, and sit again. There is little ruffling of the plumage. At this time the bird will shake its head, peck at a leaf, or the substrate, wipe its bill, but most often perform a peculiar head movement. The head and neck are rapidly placed flat on the ground in front of the individual and are simultaneously rotated a quarter-turn in one direction with the bill remaining in the axis of the straightened neck. The bird then quickly rotates its head a half-turn in the opposite direction and withdraws the head and neck. This may be repeated, or head shaking, pecking, or bill-wiping may occur. Soon the bird will turn slightly on one side and lift the upper, folded wing high over the back in such a way that it looks as though the wing were broken. As the wing approaches the midline, the tips of the primaries actually cross over the back. Enhancing the "broken wing" look is the bird's head which now rests between the body and the raised wing, specifically between the wrist of the raised wing and the breast. Again, the bird will extend and rotate the head, then withdraw it. The bird will eventually turn back to a more normal sitting position and may creep about some more and sit again, or it may remain sitting. It is not uncommon for the same side to be bathed again or the bird may alternate, but in a full bout of spraybathing both sides eventually are exposed. When a bout is over, the bird walks off slightly ruffling and then relaxing the plumage.

The odd motion of the head in spraybathing

may be better understood when looking at pool-bathing. The bird enters a shallow pool and may peck at the surface or drink. The actual bathing may begin by a lowering of the body into the water in a rhythmical bobbing motion. But this is not always seen. The bobbing wets the ventral surface of the bird. Next the body is lowered into the water tilting slightly forward on the breast. Again, the head movements occur, but the head and neck are stretched out parallel with just the tip of the bill into the water's surface. The rapid rotation throws a few drops of water some of which land on the bird's plumage. The wing is raised as in spraybathing but there is no bill wiping or head shaking, although there is sometimes a rare peck at the water's surface. These two types of bathing are not mutually exclusive and may be combined.

The plumage of both the *Crypturellus* species I observed is quite different from the other tinamous. Besides being much darker, the feathers have a dusty coating that repels water and indicates abundant powder downs (Welty, 1973). This covering washes off and remains on the surface of the water like minute bits of wax. From this I was able to tell whether a *Crypturellus* had bathed since the water pans had last been filled. I could tell which birds had bathed recently because their plumage appeared considerably darker. The color change was due to the removal of the waxy dust. The *Crypturellus* like water and would even rest in it for several minutes at a time.

The most active bather of the openland-grassland forms was *Nothura maculosa*. Under a spray of water, it goes down on its breast, throws back its wing on one side, and turns on the other. Following a period of deprivation of water spray, these birds would go down and turn with such momentum that they would roll completely over. Bump and Bump (1969) noted this species' eagerness to spraybathe. *Nothura maculosa* also bathed in puddles or pools; this was not seen at close quarters, but the birds did run purposefully into a standing puddle, stop, ruffle, crouch, and then run out again.

Rhynchotus is drawn to the spray from a hose because of the movement caused in the grass by the water, rather than by the spray itself. The birds avoid getting wet most of the time. Occasionally a bird would run through the spray or through the water pan. But on only three occasions did I see a bird hesitate in the water, ruffle its plumage, and bob up and down in the water or make a few tossing motions with the bill. Only once did a red-winged tinamou crouch in the spray and perform a few desultory dustbathing-like motions before moving on. These bouts were all very short.

Nothoprocta ornata spraybathe by going into a sitting position, rolling over on one side, fluffing the plumage, and raising the upper wing. This same procedure is then repeated on the other side.

Sunbathing

This behavior was not observed in the red-winged tinamou. *Crypturellus noctivagus* is an active sunbather. Even when light intensity was low, it went into sunbathing postures in the forced air stream from the heater, despite the fact that it was sometimes difficult to hold that position in the strong draft. *Nothoprocta ornata* would also sunbathe in response to the same stimulus. Lanyon (1958) found a similar behavior of birds in complete darkness. A spotlight would also elicit sunbathing in *Crypturellus noctivagus*. The light was strong and so close to the ground that the area under it was warm. A bird would wander under the light and seem to become caught by it, stopping directly under it and standing for a time. Then it would turn and sit and slowly roll over to one side. The wing on the upper side would then take one of two positions. Either it is raised over the back while kept folded and held in that position, or it is held fully extended out across the side of the bird and parallel to the ground. Due to the cant of the wings, only the tips of the primaries rest on the substrate. Gradually the eyes are closed and the head allowed to sink slowly until the bill rests on the ground. A sunbathing bout may be interrupted by some other maintenance behavior such as scratching the bill with the foot.

To summarize bathing behavior:

1) In captivity most openland-grassland birds do not sunbathe. *Nothoprocta ornata* is an exception. Bohl (1970) reports that *Eudromia elegans* sunbathes, which is a second exception. The non-sunbathers are exposed to the sun much of the time, while the forest birds which are active sunbathers, are not. Welty (1963) discusses the possible function of sunbathing.

2) Tinamous of the openland-grassland regions do dustbathe. They live in a drier environment than the forest forms which do not dustbathe.

3) Birds of the forest are more active waterbathers. Their environment has a higher rainfall and thus water would be more abundant. *Nothura maculosa* is an exception. *Eudromia elegans* was not seen by me to waterbathe but Bohl (1970) says that they rainbathe.

It must be kept in mind that the condition of captivity could greatly influence whether a type of bathing occurs and the degree to which it is used. Tameness, for example, can affect bathing, for only a bird that is sufficiently habituated to its environs and the presence of an observer will be relaxed enough to perform it.

Powder downs and oil glands

Welty (1963) states that birds without oil glands frequently have abundant powder downs. *Rhynchotus* has few powder downs and a large preen gland while *Crypturellus noctivagus* has

many powder downs and a small gland. Welty states further that powder downs grow in dense yellowish patches, especially on the breast, belly, or flanks of a number of birds including tinamous. In the tinamous that I have examined, these feathers seem more dense on the rump and are diffusely spread over the body. In addition, they are the same grayish color as the downy base of the feathers and aftershafts. Thus they are not easily separable.

Yawning

It is not uncommon to see the red-winged tinamou yawn, clearly displaying its wide gape. The function of yawning has been studied in other birds (Sauer, 1967). I can assign no display function to it and it does not seem to be mimetic. In *Crypturellus noctivagus* the incidence of yawning increased markedly with the starting of the heater which blew hot air into the flight. Dilger (pers. comm.) has noticed that rheas in captivity seem to yawn when jet aircraft take off in fairly close proximity to the birds, perhaps in irritation to the sound or intense vibrations.

Wing flap

Usually without warning, a *Rhynchotus rufescens* would simultaneously go up on its toes and quickly raise its half-folded wings over the back and bring them down sharply making a loud flap. This is performed by both sexes.

Variations include a double wing-flap or a jump as the wings are flapped down and finally a sharp, short cry after the flap. I was not able to determine a function for this behavior although I feel it has some aggressive display function. In *Eudromia elegans*, a similar behavior is used in aggressive encounters where one of the flapping wings hits another bird. In *Crypturellus noctivagus*, again the function is not obvious.

At least twice, when I was imitating the call of *Rhynchotus rufescens*, the dominant male stopped what he was doing and walked to a point in front of me and seemed to direct a wing flap toward me and then returned to where he had been before.

Sleeping posture and roosting behavior

Well before dark, the red-wings begin preparing for the night. Each bird has a favorite roosting place but usually a fresh roosting scrape is prepared each evening. The bird may be already resting near the site of the roosting scrape or approach it directly. If this site is in an area of abundant straw, the bird will make several turns while lifting the feet higher than usual, but sometimes these same turns are performed on bare ground. The bird may use this behavior to push down the grass and to select the actual site of the scrape. Eventually the animal settles down and performs scraping and turning motions as those of dustbathing. Some birds repeatedly select sites next to others, and might perform pushing-under bouts. These are most often females pushing underneath a bird already in its roosting scrape or in the preparation stage. These birds would commonly choose a roosting site near those birds under whom they had pushed. This behavior is reminiscent of a chick pushing under and into the plumage of a parent and would seem to be the evolutionary source for the behavior. Also at this time some precopulatory behavior occurs.

Red-wings sleep sitting with the neck in a tight "S" curve and the bill resting on the upper breast. There were only two exceptions: one bird was seen sleeping while standing on one leg; another had its head tucked under the scapulars like most other birds. It could be that these tinamous never felt relaxed enough to tuck their heads in my presence and did so after I left, or at least during a deeper part of the sleeping period.

Roosting scrapes are placed near objects such as aviary walls, vegetation, or barriers. They can further be distinguished from dusting scrapes by the abundant droppings found around their edges.

Schäfer (1954) reports that *Crypturellus noctivagus* roost in trees at night. I placed a number of perches including a small tree in their flight, but only saw perching when a bird was put to flight by an aggressive cage-mate and it would inadvertently flutter down into thick vines. I repeatedly saw *Crypturellus noctivagus* individuals take off for no apparent reason and fly to the ceiling of their enclosure and flutter down to the ground. Also the yellow-legged tinamous were the most relaxed tinamou during the day, but at night they became the most flighty. Almost any movement would send them into a panic, flying to the ceiling and fluttering down in the dark. This may indicate improper roosting facilities for this species. As mentioned earlier, other species of tinamous have been reported perching in trees at night (Skutch, 1969; and Wetmore, 1965).

Defecation

This behavior seemed elaborate and exaggerated enough to have some signal function, but my investigations did not elucidate any. It occurs most often 15 to 30 minutes after a feeding bout when an individual who is usually walking will stop, ruffle the plumage, may take a step backward, half-crouch and extend the head and neck forward, slightly raise the wings, and defecate. The bird rises, may ruffle-shake, and walk on. *Crypturellus noctivagus* commonly defecates while stretching both wings over the back. This was rare in the red-wing.

Preening

As noted earlier, *Rhynchotus* has a well-developed oil gland with a tuft of specialized feathers projecting out about 1 cm. In some individuals this appeared to be four separate tufts, in others two, and in one bird it looked like one large tuft.

Preening in the red-wing is very much like that of Anseriformes. The preen gland is pinched and the bill and head are rubbed over the surface of the body and the preening of the flight feathers, tail, and coverts was also similar to that of a duck.

Preening follows bouts of waterbathing, dustbathing, and copulation as well as most feeding bouts. Preening before preparation of the evening roost scrape was also noted.

Food, Feeding, and Drinking

The feeding apparatus

One of the peculiarities of the family Tinamidae is their broad gape. The red-wing's gape is 2.5 cm between the commissural points. In addition, this gape seems to cut deeply into the head, so when viewed from the side, the commissural point is situated well posterior to the eye. This wide gape permits the swallowing of large food items.

The bill of *Rhynchotus* is the longest in the family, tapering 4.5 cm from the forehead to the tip and almost 6 cm from the commissural point to the tip. It is dorso-ventrally flattened and slightly decurved. The tip is depressed also so that it is sharply pointed in its lateral profile and broadly rounded from above.

This bill and the bird's long, powerful neck constitute an effective digging mechanism. The toes have short rounded claws adapted for scraping and scratching the substrate. However, the scratching common in the feeding behavior of many terrestrial birds has not been observed by me in any of the tinamous. *Rhynchotus*, at times, uses its feet to scrape while feeding, but this is in an unusual way and does not function to uncover food but serves only as an accessory to the digging of the bill.

One would expect that a member of a family with an unusual bill would feed in a different way, exploiting another food source. This is indeed the case.

Diet

The red-winged tinamou can almost be classified as omnivorous, for it is capable of consuming a wide variety of food materials, the only exception perhaps being carrion. Yet the greatest quantity of its diet is vegetable matter.

Through the examination of stomach contents of 53 specimens of *Rhynchotus* taken at different times of the year from diverse areas of the state of Sao Paulo, Brazil, Hempel (1949) concluded that the principal part of their diet was vegetable material consisting mainly of tubers, tender roots, and seeds. Some fruit was present, especially *Byrsonima intermedia*, which is known locally as the "fruit of the red-wing." Another favorite fruit was guava or *aracas do campo* (*Psidium* species). Fruits and seeds of *Smilax* species, seed of *Convolvulus* and of *Desmodium* species (Papilionaceae) were also found.

The most common seeds, according to Hempel, were those of legumes (Leguminosae) and secondly those of grasses (Gramineae or Poaceae). The animal part of the diet was made up mostly of insects. Grasshoppers were the most common. Termites (*Syntermes silvestrii* and *Syntermes parallelus*), crickets, hemipterans, coleopterans, and lepidopteran chrysalises and caterpillars made up most of the remainder. Spiders and earthworms were also present. Finally, Hempel noted that during the winter when insects are scarce, the red-wing procures more vegetable food.

Schubart, et al (1965), report the stomach contents of four specimens from the state of Minas Gerais, Brazil, that varies little from Hempel's findings.

Comi (1927) and Renard (1924) found that *Rhynchotus* occasionally take mice. Comi felt it occurred more often in areas where grain was not abundant and the birds were forced to take this unusual food item.

Aviary diet

The following diet was supplied *ad libidum*: High protein pellets—Game and Turkey Grower Pellets, Agway, Inc. (21 percent crude protein). Mixed seeds—Wild Bird Seed Mix, Agway, Inc.; contains: milo, red and white millet, wheat, sunflower seeds, shelled peanuts, canary seed, and buckwheat. Growing grass of varying ages, sprouting grass seeds, clover, alfalfa, and other plants. Calcium sources—(a) cuttle bone, whole and crushed; (b) oyster shell; (c) Calcite crystals; and (d) chicken egg shell.

Regularly supplementing the above diet were the following: Fresh greens such as various types of lettuce, cabbage, mustard leaves, and spinach. Vegetables such as potato and carrot. Fruit such as apples and grapes. Live animal material: (a) earthworms, (b) mealworm beetles and larvae (*Tenebrio molitor*), (c) crickets, and (d) pillbugs (isopods).

All of the live animal food was cultured in the aviary and was available the year around. Earthworms were also collected and brought into the aviary when they were in season. New food items were continually being tried both as a supplement to their diet and to obtain information on feeding behavior.

Small sections of the aviary floor were spaded up and mixed with peat moss and kept moist. At these locations grass seed was routinely sown and it was there that the earthworms were presented. Those which were not immediately eaten would remain in these moist "oases" and were available to the birds who dug them later.

During the summer months, quantities of insects and spiders were collected with a sweep net for use as a further dietary supplement.

Feeding behavior

Rhynchotus almost always consumed live food at once. A bout of feeding could be stimulated at any time of the day and feeding times were more determined by my schedule than by any natural preference that the birds might have had. I have the impression, however, that there was generally an early morning feeding bout before 10:00 a.m., and an irregular afternoon feeding time. In addition, just before making their evening scrapes there would be increased feeding at the food bowls.

Appetitive feeding behavior is obvious as the birds actively forage while walking with their heads low to the ground. At first seeds and other food items which were broadcast over most of the flight floor were taken in preference to that offered in bowls. Random pecks, mostly into the moist areas, occurred at this time. This is exploratory or incipient digging behavior. After a period of this active foraging and feeding behavior, the bird will find a spot for digging.

Digging behavior

In a soft substrate such as moist earth, the bill, in one continuous motion, is jabbed in and brought sharply backwards by the flexion of the neck. A lateral component is added by a slight turning of the head at the same time. This causes most of the dislodged material to be thrown back and to the side at about a 45 degree angle from the body line. The side component alternates from one side to the other. If the substrate is very light and soft, as is peat moss, the bill appears to be open during the throwing part of digging.

When undisturbed in a good feeding location, the bird will crouch and continue digging. As this goes on, some debris will build up in front of the breast. The feet are then alternately brought up carefully forward to scrape this material back from the breast; at the same time, it may advance the bird's position, as the foot may not return exactly to the original resting position but to a somewhat more anterior point.

The stimulus for this slow scraping foot movement is dirt touching the breast. As a bird's breast comes in contact with the rim of a feeding bowl, the same behavior is observed. The feet come forward and scrape as though to pull down the side of the bowl.

While digging, the birds eat earthworms, grubs, ants and ant pupae, roots, and sprouted seeds. Blaauw (1896) also observed *Rhynchotus* obtaining earthworms in this manner. Digging bouts usually followed the presentation and eating of fresh earthworms. Newly-spaded earth stimulated digging also.

Jumping

In addition to digging, *Rhynchotus*, like some of the other tinamous, increases its potential three dimensional feeding space by jumping up and picking insects off vegetation. Tests to determine the limits of this ability showed that they could catch insects 1 m off the ground, although accuracy falls off markedly between 85 and 100 cm. *Crypturellus noctivagus* was similarly tested and was found to be accurate up to 75 cm.

In jumping for insects, the leap is made almost straight up, as the animal positions itself almost directly in front of the item to be taken. This differs from agonistic jumping which has a much greater horizontal component.

Handling of food items

Very small items such as rye grass seed, clover seed, small ants, and flour beetles (*Tribolium confusum*) are not eaten, while things slightly larger such as canary seed and millet are taken readily. Most insects, seeds, pellets, and other food types are handled in much the same way. The object is pecked and seized between the tips of the mandibles. The head is withdrawn, and then thrust forward as the bill is opened and the item is thrown into the gullet. More precisely, the gaping mouth is thrown around the food object.

When several small food bits are collected in the mouth, they are swallowed. Larger food items are downed whole and swallowed separately. One of the largest items taken in this way was a cerambycid beetle, *Prionus* species, which measured about 3.8 cm long and 1 cm wide.

Sunflower seeds may be shelled, especially if the seed has lain on damp soil and softened. These seeds are tested by a loud clicking mandibulation. If the mandibulation continues, the seed may be hulled, eaten whole or it may be dropped. Shelled peanuts, even though smaller than items swallowed whole, are commonly broken up, by one or two pecks and the pieces are then consumed one at a time.

Seeds are usually eaten off the ground, but I did see birds taking seeds from maturing grass heads. Also the red-wings do eat some blades of grass and leaves, especially new growth, but they concentrate more on the roots and shoots which they expose while digging.

Small earthworms 5 cm or less are swallowed whole. Sometimes when tossed, not all the worm goes into the gullet and another swallowing act is required. The larger earthworms will not fit in the mouth and therefore require several swallowing attempts. Most commonly the large earthworms (*Lumbricus* species) are pecked and given one or more shakes and snipped in two. There is some variation in whether these shakes included rubbing the worm on the ground. The largest are commonly given these sharp shakes while being held against the ground. These worms are usually snipped into three pieces before being ingested.

The birds show a preference for the smaller worms.

An interesting example of special handling before eating is the treatment dealt to the woolly bear caterpillars (Arctiidae, *Isia isabella*). The larva is quickly grasped and at the same instant the bill makes rapid lateral motions in the substrate in an arc about 5 cm long. The larva is dropped, picked up, and rubbed again. If the substrate is gravel, the bird will attempt to rub the item, but then move to a finer substrate. When most of the setae are rubbed off, the larva is thrown into the maw and swallowed. A remarkably similar behavior was reported by Morton (1968) in robins which were feeding on the same larvae. A food source which is rejected by most birds but is eaten readily by *Rhynchotus* is slugs (*Limax*, *Arion*, and *Deroceras* species). Centipedes, millipedes, as well as terrestrial snails are swallowed whole.

The birds would not eat carrion, canned dog food, or chopped or stripped fresh calves liver. The stripped liver was rejected even when thrown out to the birds alternately with earthworms of the same size and dimensions.

I have seen *Rhynchotus* and *Crypturellus noctivagus* chase and catch low flying insects when they land, but these again have to be above a certain minimum size to be of interest. Their catching moths has been most conspicuous.

The red-winged tinamou is an extremely opportunistic feeder and can capitalize on an abundant food source by shifting its intake temporarily and almost exclusively to whatever is plentiful. This was seen many times in the aviary and is illustrated by the study of stomach contents by Hempel (1949). He counted 45 grasshoppers in the stomach of one bird, 275 termites (*Syntermes* species) in another, and 707 in a third. Liebermann (1935) claims that *Rhynchotus*, like most other tinamous, eats locusts (grasshoppers) and that during times of locust invasions (grasshopper outbreaks), the red-wings eat little else. In the aviary it seemed virtually impossible to satiate these birds with live material. In one morning the six individuals had eaten over 1 kg of earthworms and they were by no means equally distributed among them. Perhaps not all the protein is available to the bird's metabolism from an eating orgy such as this, for after such excesses I would find very dark blackish-brown droppings of the consistency of heavy grease. Mealworm larvae are always eaten in any quantity provided, as are crickets. Because of this voracious appetite, attempts to establish ant colonies and cockroaches in the aviary were unsuccessful.

Predation on vertebrates

From the reports of mouse eating in the literature (Comi, 1927; and Renard, 1924), I tried presenting small mice to the birds. They proved to be determined, if not well-equipped, predators. Although able to deliver hard-driving pecks, they seem unable to break the skin of even a mouse. They are likewise unable to subdivide the flesh. Thus, it takes them a long time to kill an animal and quite a long period of repeatedly pecking the carcass until it is swallowed. At that point the carcass is very limp and soft. It is taken head first and the first thrust of swallowing lodges the mouse's head within the mouth of the bird. After a long bout of swallowing, the tail of the mouse finally disappears.

A 30 cm garter snake (*Thamnophis* species) was brought into the aviary to check the reaction of the birds. At first the birds were quite put off by the coiling and striking behavior, but soon they were pecking at it, mostly on the tail, and running with it. When dropped, the snake covered its head with its body so many of the pecks were not too detrimental. The snake was taken back and forth through the aviary by various birds, one snatching it from another. Eventually the snake, though not quite dead, was eaten head first, again requiring a long bout of swallowing. Later, snakes up to 35 cm long and of various species (mostly *Thamnophis* species and one milk snake, *Lampropeltis doliata*) were eaten with less expenditure of energy and the snakes were much more alive when swallowed. One individual swallowed two snakes tail first. Both of these tried to crawl out or at least stop the downward motion toward the bird's stomach without success. When the snakes approach 30 cm in length, a peculiar problem arises. When running with the snake, unless it has been grasped near the middle, it will be stepped on by the bird's foot which pulls it out of the bird's mouth. The snake is quickly grabbed by another bird, only to have the same thing happen.

After a bird has swallowed a large animal, such as a snake or mouse, it assumes a "full posture." This is a crouch in which the body is held more upright, and the head and neck are maneuvered out, down, and up, apparently to aid in the passage of the consumed animal down the throat and into the crop.

There was never any sign of regurgitated bones, nor was there any bone or hair in the droppings, so I assume that the birds are capable of digesting these items.

Other vertebrates taken as food include small frogs (*Rana pipiens* and *Rana clamitans*) and toads (*Bufo americanus*). Although somewhat similar in appearance, these were dealt with in different ways. The frogs were treated in the same way as the mouse, with repeated hard pecks; but the toads were pecked and rubbed in the dirt, pecked again and rubbed again, and finally swallowed head first. The toads less than 2.5 cm are pecked and swallowed whole. Tadpoles were also taken from the water pan.

These birds had a tendency to eat their own eggs, especially if they were laid outside the nest area. A chicken egg placed in the middle of the aviary was eaten by the end of the second day. Five dove eggs were placed in a small depression on the ground and were eaten in one afternoon. Five *Coturnix* quail eggs, which have a mottled brown color pattern, remained for several days without being touched and were then removed.

In general then, *Rhynchotus* differs from the other openland-grassland tinamous in the degree to which it feeds on material found under ground and its almost complete lack of grazing on mature grass leaves. *Eudromia elegans*, *Nothura maculosa*, *Nothoprocta ornata*, *Nothoprocta pentlandii*, and *Nothoprocta perdicaria* are all grazers and probe only shallowly into the ground. They are most apt to turn over small rocks. *Crypturellus noctivagus* and *Crypturellus obsoletus* are leaf turners and tossers.

Rhynchotus was never seen to eat feathers, while *Crypturellus noctivagus* does eat them. Hempel (1949) found feathers in the stomach of *Crypturellus parvirostris*.

Drinking

Although water was provided *ad libidum*, the tinamous drank very little, except when they were sick and long bouts of drinking occurred. Drinking behavior is scattered quite evenly throughout the day and it is very uncommon to see one individual drink more than once a day.

Drinking in the red-wing is always from standing water and never from the foliage as with *Nothura maculosa*, *Nothoprocta perdicaria*, and *Nothoprocta pentlandii*. These two *Nothoprocta* species seem to prefer drinking from the foliage rather than from the water pan. Koepcke (1963) noted this preference in *Nothoprocta pentlandii*.

Rhynchotus dips its bill into the water at a very low angle. There is some variation in how deep the bill is immersed in the water, but it is usually about 1 cm. The gullar area is moved in and out and the head is raised high. This may be repeated up to three or four times.

Agonistic Behavior

The red-winged tinamou, it was noted, is a bird of the tall, open grasslands. Hudson (1920) somewhat ambiguously describes them as being solitary and yet with "many birds usually found living near each other." I assume this latter statement was made on the basis of his hearing "many individuals answering each other" during periods of calling.

Rhynchotus, then, lives in a rather dense environment of tall, tufted, or clumped grasses and is in at least auditory contact with several neighbors during parts of the day.

The area available for an individual's home range would probably be measured in hectares and not in square meters as in the aviary. Marler and Hamilton (1966) state that crowding can affect dominance systems and that in many captive vertebrates a shift from territorial dominance to individual dominance is seen as densities increase. My findings support this.

The crest

All of the tinamous I observed have erectile crests, but only in *Eudromia*, the crested tinamous, have these markedly specialized, forming a graduated crest about 5 cm long. It is undoubtedly not coincidental that in the tinamids this well developed, highly mobile, visual signal is found in the only species which is known to occur in flocks (Wetmore, 1926). These birds display a flock cohesiveness which I have not seen in other tinamous. The movements of one individual at times are determined completely by the movements of the others, especially when they are disturbed. This is unlike the other tinamous which, if they happen to be together, are most apt to disperse when alarmed.

The red-wing's crest feathers are black, streaked with tawny brown. When viewed from *Rhynchotus* eye-level, the erected crest appears mostly black. These feathers are about 1 cm long, shorter on the forehead and longer on the back of the head. Thus, when fully erect, there results a marked increase in the apparent size of the head.

As has been demonstrated in a wide variety of birds, the position of these feathers can change quickly, showing the fluctuations in the motivations of the bird. Crest-raising or crest-up indicates aggressive motivation while crest-lowering or crest-down is a sign of fear. Within a few seconds the crest can change from one extreme to the other. This is predictably seen, for instance, when the birds are drawn into a small area by a concentration of a favorite food item such as mealworms.

The crest plays an important role in the routine display of dominance and submission. A meeting between a dominant and a submissive bird results in the dominant one raising its head and crest, while the submissive bird lowers its head and may sleek the crest. Also, when one individual chases another, the pursuer has its crest raised most of the time and the fleeing bird's head is usually sleeked.

These birds are capable of individual recognition which is obvious from the dominance hierarchies which are formed. These hierarchies are not often linear and can change rapidly during the reproductive period. An indication of the importance of the crest in the role of dominance may be illustrated by the fact that the least dominant bird was a male which had had the top of his head skinned and lacked a crest. Eventually when he tried to exert himself aggressively, he used one of the more extreme displays not entail-

ing the use of the crest, but even then it appeared that he was ignored by the other birds.

This could imply that in *Rhynchotus* learning plays an important part in aggressive encounters, as has been shown in other vertebrates (Marler and Hamilton, 1966). An obvious explanation might be that an individual unable to display day-to-day dominant aggression toward any of the other red-wings eventually loses his aggressive identity. Thus on occasions when this bird without a crest was very aggressively motivated and used extreme threat displays, other red-wings would apparently feel no fear and make no effort to avoid him.

Threat displays

The threat displays of the red-wing may be scaled in order of the degree of their aggressiveness. Starting with the least aggressive, they are as follows:

1) The mildest threat is when one individual orients its head toward another. The threatening bird may be sitting, crouching, standing, or walking. If walking, the bird usually stops as it orients the head in threat. The head may be turned in any direction, even posteriorly over the back.

2) If the neck is slightly withdrawn and the bill opened as the bird orients toward another, a higher degree of threat is indicated. This can be given from a standing or sitting position and is most often directed anteriorly or laterally. Peck feigning is probably an extension of this and is discussed below.

3) A much more extreme threat is displayed when, added to the above attitude of neck pulled in and gaping bill, the bird orients the body and assumes a crouched or nearly crouched position. This is a forward leaning posture and it varies in the degree to which the bird goes forward and down on its breast. In the most threatening form, the bird's breast touches the ground. From this position, a bird can easily jump at an opponent. It is similar to the threat of the common rhea (*Rhea americana*) as described by Raikow (1969). The rhea, however, is more nearly in a standing position. *Crypturellus noctivagus* is more rhea-like in its standing posture but it does not gape. It alternates this tilted forward, neck withdrawn posture with a few stalking steps toward the bird on which it is oriented.

4) If the above threat display of *Rhynchotus* is not readily effective and the offending bird continues to approach or remains nearby, another component is added. The aggressive bird goes into a full forward crouch with the breast on the ground and the feathers of the rump begin to rise in broad plaques of twos and threes.

5) Finally, the highest level of threat is for a crouched bird, leaning forward on its breast, neck withdrawn, bill gaped and rump feathers elevating, to give a soft shrill cry as though to call further attention to itself and accent its aggressive state.

Only males go beyond level 3 and it is rare for a female to perform at a low level 3.

Peck feigning is related to level 2 in the aggressive scale above, but it is most used in fast moving, transient encounters when an aggressive bird with little time to react makes an irresolute attempt to peck an intruder. Many times the bird is sitting and the peck attempt is obviously futile since the bird would have had to move in order to land the blow, as for example when the feigned peck is directed posteriorly over the back at an intruder.

Overt aggression in the red-wing is restricted to pecking and/or chasing another bird. Chasing is usually a short burst of running that rarely goes beyond 3 to 5 m. Longer distances are covered by interspersing chasing bouts with walking pursuits.

Pecks are mainly directed at the rump and back of another bird. These are hard enough to be audible but in the red-wing, they do not often result in the loss of feathers. In *Crypturellus noctivagus* an aggressive peck is commonly combined with feather plucking. After a chase and peck, the aggressive bird is left standing with a contour feather in its bill while the other bird runs off. After a pause, the plucked feather is carefully mandibulated and then ingested, calamus first. The assailant seems surprised and distracted by the presence of this object in its bill, and pauses as though to "decide" what to do with it. Perhaps other *Crypturellus* species do this as well for, as noted earlier, Hempel (1949) reports feathers in the stomach of *Crypturellus parvirostris*.

Figure 3 is a graph showing the frequencies of overt aggression and threat displays according to the sex of the aggressor and the individual eliciting that aggression. The most common encounters are males displaying aggression toward females.

I had assumed that the most common encounters would be male-male interactions as would be true for many vertebrates so confined. I expected that the males might do little else than fight among themselves, and watched carefully for any indication that they might injure one another.

Lancaster's observation (1964) of *Nothoprocta cinerascens* that the only means of territorial defense by the male is calling bouts, may give an indication as to the paucity of chases, pecks and visual threat displays between red-wing males. This will be discussed further in the section dealing with vocalizations. The lack of much female-female interaction was about what I expected.

The similarity of frequencies of threats, male-to-male, female-to-female, and female-to-male is remarkable and in sharp contrast to that of males-to-females by seven-fold. This does not mean that the males can readily distinguish between the

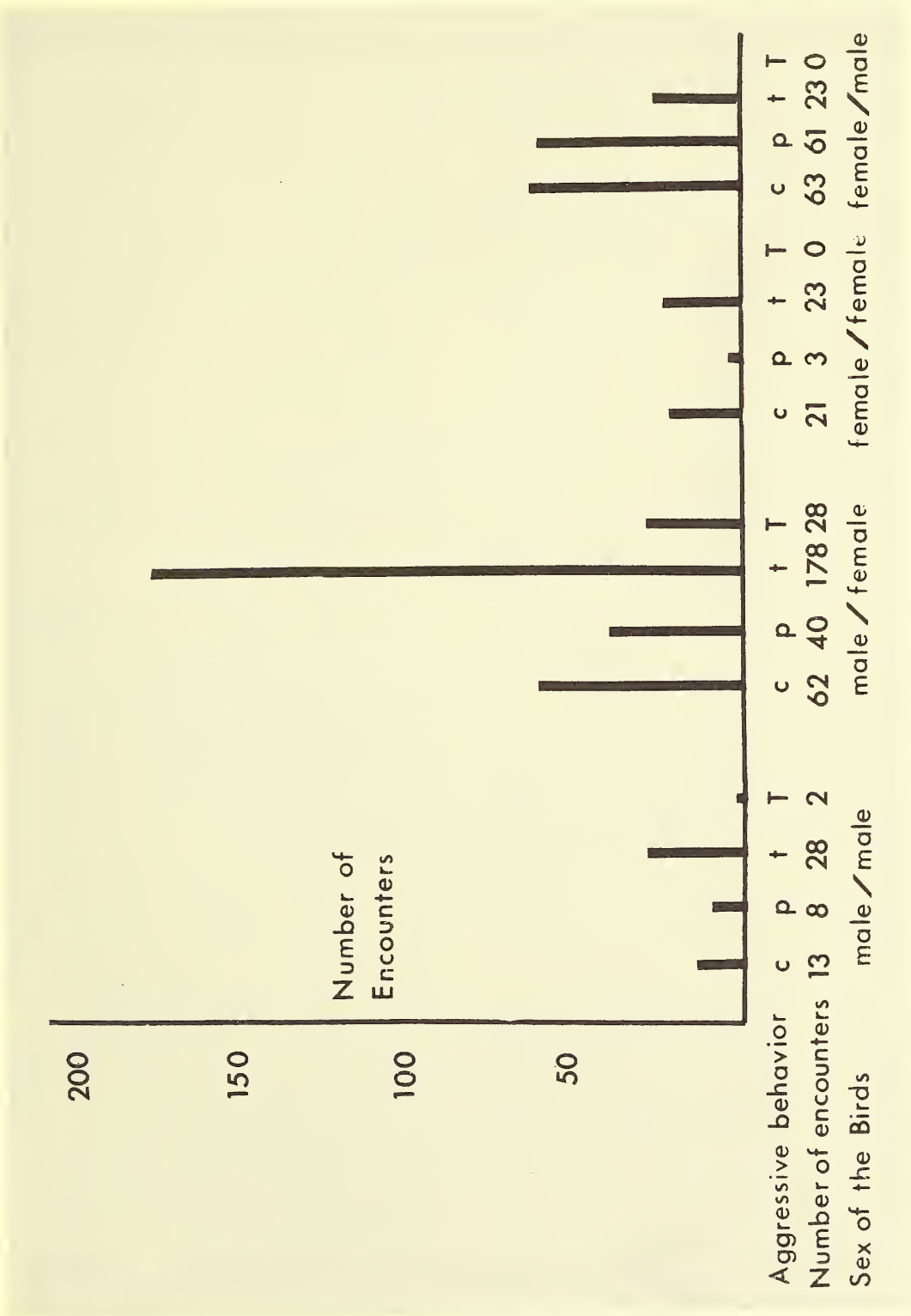

FIGURE 3. Distribution of aggressive encounters of *Rhynchotus rufescens* by sex. Aggressive behavior: c - chase p - peck t - threat T - high intensity threat.

sexes in this monomorphic species. It is much more an indication of the persistence of females in staying close to aggressive males, as occurs periodically throughout the breeding season. The response of threat and high intensity threat of males may be a sexually diethic clue to the females as to whom to follow.

The high incidence of chases and pecks which females use toward males, as shown on the graph, may be misrepresentative of their relative aggressiveness.

It appeared to me that some of the pecking behavior of females directed at males was not entirely aggressive. These pecks were not restricted to the back or rump of the male, and were more often aimed at the side of the body, neck, and even the head. The female was usually quite close to a resting male at these times and it was difficult to determine the strength of the blow, but the males did not respond as though pecked aggressively. Most aggressive pecks are delivered to birds which are running or starting to run away. Commonly there was no immediate visible reaction by the male having received one of these female pecks, but such a male would soon be moving about with the female closely following.

As stated earlier, the wing flap and jump-wing flap may have aggressive display value in *Rhynchotus*. Males performed 62 percent of them, and one-third of these resulted in a female leaving the male's immediate area. Males were never seen leaving the site of a wing flap or jump-wing flap. Females never caused other birds to leave with this behavior.

Also mentioned earlier was the fact that jumping can be used in aggressive encounters. Only rarely was a jump used by an aggressive bird; it was seen most often as a means of escaping aggression. Agonistic jumps have a strong horizontal component and an individual can easily move 0.5 to 1 m in any direction without clearing the ground by more than 15 to 20 cm.

Reproductive Behavior

Because of a wide variation among individuals of both sexes, it is difficult to give a clear, concise description of a typical breeding cycle.

Although aviary acclimated birds, in residence for at least a year, will produce a few eggs through the winter, the active breeding season starts in early March. At this time the previously brief aggressive encounters become more frequent and intense. Most obvious, however, is the increase in male-chasing-female pursuits.

The dominant male is responsible for much of this aggression and it is customarily directed at one female. These aggressive periods last one to two days. Then the male gradually shifts to less aggressive behavior. Perhaps then a calling bout follows or the male may begin to approach and follow the female toward which he had been aggressive. Then they forage and feed together frequently. This approach and following behavior can subtly change into a driving behavior of the female and, during the transition, it is almost impossible to determine which bird initiates the action.

Late in the evening, in early spring near the first week in March, there begins some precopulatory and incipient copulatory behavior among the birds which roost or attempt to roost close together. This sexual behavior is performed by males and each evening it begins a little earlier. A male approaches and crouches breast to breast against another bird which is usually sitting. As he pushes, his wings are flared downward and held slightly out from the body. This displays the contrasting rufous color of the primaries and I call it wing-flaring. The male most commonly pushes against a female; a female is usually nearest at hand. At first, birds run off when pushed, although they return in a short time. When females are gone, the wing-flaring male will move to push against another male. Wing-flaring is elicited from a sexually motivated male by the sight of a sitting bird.

After several evenings of wing-flaring and pushing, a new component is added. At the end of a bout of pushing and flaring, the wings are brought back to normal position, and the wings then tremble and the bird may move slightly backwards. This may be seen several times after a bout of pushing and it gradually increases in intensity. Perhaps as the bird is pausing between scraping bouts while working on his roosting site, the same wing-trembling and scooting backward behavior is seen. As the bird moves backward, the head and neck are extended horizontally. Also it can be seen as well as heard at this time that, as the bird moves backward, the feet are drummed on the ground. The movement of the body must be accomplished by a backward shuffling of the tarsi with most of the weight on the heel joint. I term this behavior tremble-shoving. As soon as copulation occurs, it becomes part of copulation and post copulatory behavior.

Copulation also starts as a late afternoon, early evening behavior and gradually occurs earlier each day. The male approaches the sitting female as before, pushing against her with the wings flared. Eventually the male will step up on the back of the female. The first copulations of the season usually display a great amount of ineptitude, with an apparently nervous female, and the male slipping off only to flare his wings and remount. Figure 4 shows a male with his wings flared and mounting a female.

By the middle of April, copulatory behavior can occur almost any time during the day and takes place as often in the morning as in the afternoon. Pairs which have copulated together more frequently seem to be more adept, and this be-

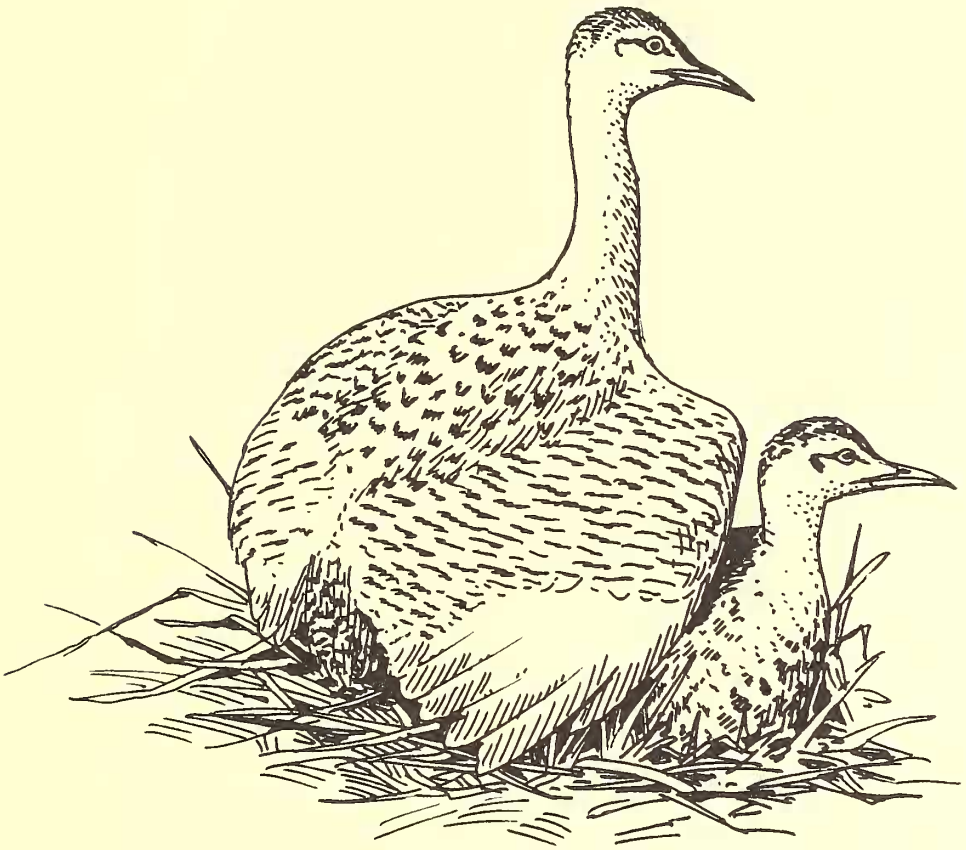

FIGURE 4. *Rhynchotus rufescens* male wing-flaring and mounting a female.

havior proceeds in a more regular fashion.

When copulation becomes an activity which can occur any time of the day and the males are simply mounting roosting females, another precopulatory behavior is seen. Males now approach females which have demonstrated their receptivity by staying close to the males. These pairs usually perform a bout of circling before copulation. Circling is the culmination of a prolonged period when the females would initially avoid males but, after a time, start to circle around behind one and stay behind him. If she should get in front of him by her moving, or more commonly, by his turning, she is then obliged to circle around him again or be threatened. Gradually circling becomes tighter and tighter until the female is simply stepping around the male to stay behind him. Circling, then, is the result of a submissive female trying to stay behind the male who is sexually motivated and trying to get behind or next to a female in order to mount. They move around side-by-side, head-to-tail. If circling is drawn out, the male will stop walking and only pivot on the spot as the female continues to circle him. Most circling bouts are quite short and may be interrupted by the female's moving away to another location, only to circle again with the approaching male. Only a few times was circling seen when mounting did not follow.

The male has a creeping walk, crouch, and sitting behavior which I think is similar in motivation to circling, crouching, and sitting in the female. This was seen only a few times and could be elicited during the breeding season by a series of loudly whistled imitations of the red-wing's call. The dominant male would answer a few times but then would approach a female by creeping up to her, crouching and sitting. If the female were approaching him, he would simply sit. I interpret this as a very submissive response to a supernormal, aggressive stimuli, the model in this case exceeding the normal vocalizations in loudness and in frequency of repetition.

Generally, a circling female will begin to lower her body into a near crouch. She may start this before the first complete revolution, if she is sexually motivated and not to fearful of the male. As the female goes down, the male begins to wing-flare. When she stops and sits, the male immediately tries to mount. At the first touch of the male's foot on her back, it is not uncommon for the female to begin circling again.

Eventually the male mounts a seated female with his wings flared. If he has good footing, he may crouch with wings folded from 30 seconds to as much as a minute. Rarely a male will gently peck at the female's head.

At times the female is apparently restless which may result from her being uncomfortable. For instance, this seems to be the case when she is mounted while on a gravel substrate. At times like this, she is able, with the male on her back, to shuffle along on her tarsi a meter at a time between rests. This makes an unstable perch for the male which usually responds by moving forward on the female's back until one foot rests at the base of her neck. This causes her breast to be pushed to the ground, impeding further movement.

Anytime a mounted male appears to have poor footing and is having trouble maintaining his balance, wing-flaring may occur. If the male should slide off, a short bout of circling, wing-flaring, and mounting follows almost immediately. If the female does not get up, circling, of course, does not occur.

Once seated on a stationary female and after the customary pause, the male begins treading. He alternately moves the feet which rest just posterior to the female's shoulders. Treading bouts are followed by periods of rest. Sometimes the stimulus for treading appears to be the male's foot sliding off the side of the female and treading seems to function to regain a firm footing. Generally, however, the female controls treading by the position of her head. A mounted male sits so that his breast rests against the back of the female's head. Not long after being mounted, she will swing her head and neck to one side. The male treads and turns to that side until her head is positioned on his breast again. Then she will turn her head in the other direction and again the male treads and shifts to maintain the head contact.

The functions of treading are not obvious but there appear to be several. It may help the male to get a good footing. The shifting of his weight from one side of the female's body to the other seems to allow her to get into a comfortable position. She remains quite mobile and it is common for a female to turn around during precopulatory treading. Also this functions, as do most precopulatory behaviors, to synchronize and coordinate activities leading to a successful copulation.

Several times a male well along in precopulatory stages was dislodged from one female and mounted another. With the succeeding female, the male left out the treading bouts. These mountings were always abortive, never resulting in successful copulation.

Soon after treading begins, the feathers on the male's rump begin to rise very slowly, indicating the start of the final stage of precopulatory activities. When the feathers are erected, the treading and resting bouts cease and the male begins to perform tremble-shoving on the female's back. Each tremble-shove is accompanied by the female's pushing her head back. After several tremble-shoves, the female flips up her tail and vent region to a nearly vertical position just as the male shoves backward. Very brief cloacal contacts are made at this time, as the male's vent and tail area is depressed.

From the time that the male erects his rump feathers, his swollen cloaca is visible from behind and it disappears only during those instants of coition. The female's cloaca may be seen just before being obscured by the male's tail. At no time was an intromittent organ visible. And it may be mentioned again that I was not able to determine the sex of these birds by cloacal examination, nor was I able to evert an intromittent organ on any of the males.

It was possible, however, when viewing copulating birds from behind to determine if and when sperm transmission had taken place. A white, sticky viscous matter would appear within the male's cloaca; then, after a tremble-shoving sequence, just as the female's tail was going down, the flash of white indicated that it had been transferred to her. Again, the male's cloaca was mostly free of this material, which I presume was semen.

Tremble-shoving bouts last from five to 10 minutes. Initially they occur with a frequency of six per minute and may remain at this rate or drop to as low as three per minute near the end.

The copulation ends with the male dismounting, commonly by falling or slipping off the side, sometimes over the front of the female, rarely by stepping off. The female rises and begins to move off at once; after a few yards she ruffle-shakes and proceeds to a point well away from the male for a bout of preening. The male moves very little at first and seems to become, from time to time, convulsively caught up in bouts of tremble-shoving.

A similar behavior was described by Lancaster (1964) in *Nothoprocta cinerascens* males which he called ejaculatory crouches. Upon inspection of sites where tremble-shoving took place, I could find nothing to suggest that ejaculation had taken place.

The amount of tremble-shoving seemed inversely proportional to the success of the copulation which preceded. Several times when copulations were seen to proceed smoothly and sperm transmission to occur several times, the amount of tremble-shoving was minimal. The more fitful the copulation attempt, the more tremble-shoving occurred.

From mounting to dismounting, the average red-wing copulation lasts just over 15 minutes. This appears to be considerably longer than those copulations seen in the other species. Copulation in *Eudromia elegans* in only one observation lasted less than one minute. The male was seen to hesitate with one foot on the female's back, then he mounted. The treading was rapid, causing the female to rock gently from side to side. Then the male quickly slid back over the female's posterior and only one very brief cloacal contact was made. Bohl (1970) describes a circling behavior that precedes copulation in *Eudromia elegans*. In *Crypturellus noctivagus*, the bouts were longer but never more than a few minutes. In this species the wing-flicking female leads the male who may give a soft repetitive call. She crouches as she walks; the male mounts her when she stops; and he treads. The treading becomes faster and faster until the female tilts forward and raises her tail. This occurs with such momentum that after an extremely brief cloacal contact the male seems to be catapulted over the female's head.

G. Bourne (pers. comm.) has observed copulation in *Crypturellus soui* in the field, and describes a short sequence of a few minutes in which a male mounts a crouching (soliciting) female and holds onto her head feathers with his bill. A very few treading movements were followed by copulation. The male dismounted from the side and the pair foraged together for a short time afterward.

The length of the spotted nothura's copulation bouts are also short in comparison to those of the red-winged tinamou. In this species the mounted male stands on the female's back, not in a crouched position, and pecks at her head. The female moves her head from side to side something like the red-wing female, only there is no contact between the spotted nothura female's head and the male's breast. The male begins treading and wing-flicking and this gradually becomes more intense. The wings flare downward as the male crouches. After a series of wing-flaring crouches, he grasps the female's neck feathers in his bill. She usually begins to move and is carrying the male as cloacal contact is made. When the male dismounts both birds are extremely fluffed. The female has a postcopulatory display; she head pumps while standing close to the male. The male's intromissive organ is visible at this time and it appears to be about 0.5 cm long. At times it appears to move in and out. Most of these details of copulation in *Nothura maculosa* agree with those of Bump and Bump (1969) on the same species and are similar to their observation on *Nothura darwinii* as well.

In *Nothoprocta perdicaria*, the male also wing-flicks, but his treading movements are the lightest I have seen in the tinamous. The wing-flicking and treading continue until the female raises her tail. This seems to cause the male to stop and crouch backwards. The female may move at this time or stand still, and the male gets extremely far back on the female's rump. Due to the distance, however, I was never able to see the position of the male's feet at this time. Finally, the male displays a very long intromittent organ and head bobs as the female walks around him. Again, the entire bout lasts only a few minutes.

Lancaster (1964) details mounting and copulation in *Nothoprocta cinerascens*. The average bout lasts slightly over two minutes.

The nest

The factors determining nest site selection in

Rhynchotus rufescens were not clearly elucidated by this study. Nests were located at the base of artificial grass clumps and next to the walls where there was thick foliage. Their preference for high tufted grass and other vegetation as a nest site was noted by Blaauw (1896) and illustrated by Pereyra (1938).

Before egg laying begins, the sites where nests later occur are favorite loafing spots, frequently visited by pairs and by males alone, rarely by females alone. At this time each female has a loose attachment to one of the males. The pushing-under behavior of the female was seen on future nest sites, but it was also seen on areas where no nests developed. The nest occurs, then, at a location where the male has rested with and without a female. The female has usually followed him to these sites. In this way, I assume, the male is probably responsible for nest site selection. Bartlett (1868) and Blaauw (1896) summarily attribute this duty, as well as nest building, to the male.

In addition to the vegetation, the nest sites were also areas where there was abundant hay and straw. The nest begins as a rudimentary scrape and develops as the eggs are laid in it. Both males and females work on the nest. Females while on the nest to lay will pull in bits of straw and other material. The male seems a bit more active and will pull down grass from the adjacent grass clump which then overlays a part of the nest.

The fully developed nest with a clutch of eggs was well-rounded, 30 cm in its outside diameter and 18 cm in the inside diameter. The entire nest bowl was covered with straw and lined with feathers. This is somewhat more elaborate than those nests found in the field, for example, by Hudson (1920) who described them as a scrape with a small quantity of grass lining.

Within a period of 24 hours preceding the laying of an egg, the female begins to approach and follow a male. This attachment was more obvious in some females than in others, and its intensity diminishes as the breeding season progresses.

It appears that a female will not go to the nest and lay an egg without a male to accompany her. Sometimes the males seem very uninterested, even antagonistic, toward such a female which eventually gets quite frantic and runs around nervously.

Sometimes two females would go to the nest and lay at the same time or within a few minutes of each other. This synchronous laying of females can produce a large clutch of eggs in a relatively short time. About 20 percent of the eggs were laid synchronously. Sometimes two females would enter the nest but only one would lay. Sometimes the sponsoring male would enter the nest with the female or females. The impression was that the birds liked this close contact around the nest. On the average it takes a female upon entering the nest 11 minutes to lay and leave. While sitting, the females perform some nest building. Also, upon leaving, they may make a slight effort to cover the eggs by pulling bits and pieces of straw and hay over them. This is never very effective, however.

I was not able to determine clutch size from this study. Reports in the literature vary from as few as four (Barrows, 1884) to as many as 10 to 12 (Bartlett, 1868). Most reports are in close agreement with Pereyra (1938), who gives seven to eight eggs as the clutch size.

Blaauw (1868) states that females lay every other day. The females I observed could lay this often but not for very long periods. For example, one female would produce four eggs in eight days and then not lay for five days.

At various times during the breeding season, one of the males would become extremely aggressive toward all the females and would frequently use high intensity threats. These periods were transitory and lasted only a day at most. Perhaps in the wild a male drives the females off after he has his clutch. This behavior in the aviary did not seem to correlate with clutch size, however.

Occasionally the dominant male would become broody and sit on the eggs but never longer than 30 minutes. Once I saw him crouch and spread out over some fairly smooth stones as though to brood them but for only a few seconds. Casals (1940) mentions the difficulty of getting captive male red-wings to incubate.

Finally, the very submissive male took over a clutch of 10 eggs and sat very tight. When this bird did leave the nest without being frightened off, he carefully raised and pulled straw and feathers over all the eggs before high stepping away. An incubating male off his nest is very busy. This was one of the few times I saw *Rhynchotus* waterbathe. Brief bouts of dustbathing occur, as well as drinking and feeding.

Both *Eudromia elegans* and *Crypturellus noctivagus* cover their eggs as they leave the nest. *Crypturellus* is by far the most effective and it requires several minutes for a male to finish this job. The nest is completely obscured with dead leaves, feathers, and other debris within easy reach of the nest. A mat of 1 to 2.5 cm thick not only camouflages the nest but might keep the eggs warm and dry for some time in the bird's absence.

Bartlett (1868) says 21 days is the incubation period for *Rhynchotus*, and Blaauw (1896) agrees closely, setting it between 20 and 21 days. Though I was unable to determine the exact day of the onset of incubation, it was within about this time period that the male hatched one chick.

When approached within five feet, the male which was brooding the chick would rear forward, fully spreading his wings and tilting them for-

ward. In this manner he came toward me slowly, giving a cry.

I was similarly threatened by a brooding *Eudromia elegans*. He got off his nest and extended the wings out and tilted them so far forward that the leading edge of the primaries made loud scraping sounds on the ground as he moved. At one point he took several quick steps toward me in this posture. Wetmore (1926) describes a distraction display of the male *Eudromia elegans* with young in which the male flaps away on its breast. Skutch (1963) describes a male *Crypturellus soui* with eggs; the male, when put off the nest, drooped and quivered its wings and walked slowly past the observer. *Crypturellus noctivagus* defends his young much as does *Rhynchotus* with flared wings tilted forward and deliberate steps toward the intruder.

All three of the *Rhynchotus* males developed incubation patches to some degree. These could be seen as a ventral "crease" in the lower breast and belly plumage. This brood patch shows clearly in a photograph published by Seth-Smith (1930) of a male red-wing with a brood.

Care of young

The male was so wary with the young that I was not able to observe much in the way of interaction between them.

Blaauw (1896) mentions that the male red-wing presents food to the young. And Skutch (1963) saw a male *Crypturellus soui* with a chick pick up an insect, mandibulate it while calling softly, then appear to lay it on the ground. Bump and Bump (1969) state that the male *Nothura maculosa* with young will vocalize, pick up food, and drop it. I saw the male red-wing feeding from a bowl of mealworms which always before had been eaten with great voracity without ceasing until all were consumed. This time, he ate a few, then picked up one and mandibulated it in front of the chick. I was not aware of any vocalizations. The chick pecked at the male's bill, but I was not able to determine whether the food was actually obtained by the chick. This interaction between parent and chick is reminiscent of some gallinaceous birds (Stokes, 1971; and Delacour, 1951), but in this order it is usually the female that is with the young.

The male *Rhynchotus* has a soft, wavering, repetitive, descending call for the chick which usually causes the chick to approach or follow him. When disturbed, the male with a chick performs a head bobbing movement by stretching the neck up and out at a 45 degree angle, and then lowering it while slightly withdrawing and then extending the neck, stopping at a nearly horizontal position. This is repeated several times and may cause the chick to "freeze."

Vocalizations

Compared with the more social *Eudromia elegans*, the red-wing has a rather limited vocal repertoire. Perhaps this is another indication of the solitary nature of *Rhynchotus*. Comparably, however, the vocalizations of *Crypturellus noctivagus* seem even simpler, but this species has relied more on visual communications.

The advertising call of the red-wing, which I refer to as the call, was not heard when the birds were kept together in the same open enclosure. When visual barriers were erected, the introductory note, seen as the chevron pattern on the audiospectrogram (figure 5), was given alone and occasionally a very muted, stifled note followed. It was common for one of the males to go behind a barrier before giving this single note.

By a whistled imitation of this introductory note, I was able to elicit aggression. Some of the *Nothoprocta* species and *Eudromia elegans* have a loud, somewhat similar sounding, vocalization which produced the same effect on *Rhynchotus*. If two red-wings were within several feet of each other, this would most often result in a chase and an attempted peck.

This aggression would bring an end to two birds peacefully feeding or resting together. Sometimes a *Eudromia elegans* would "answer" a red-wing's introductory note before it could complete its call. These interspecific reactions may have upset the birds enough to interfere with their breeding.

As stated earlier, a prolonged series of imitated, loud repetitions would cause a previously aggressive male to perform a creeping walk, crouch, and sit. If a female approached him, he would simply sit. This behavior was never seen at any time other than immediately after the presentation of a series of these auditory models and was not seen after the presentation of other loud sounds in series. Because of its disruptive effect on the breeding of these birds, I did not test it further.

Granting an aggressive function to this vocalization and model, and noting the resemblance of this response by the males to soliciting for copulation of females, it would seem that the red-wing males, like many other vertebrates, may use soliciting behavior to avert or reduce aggression.

Close contact with another male is apparently inhibiting to calling, for complete calls were not heard until males were penned off by themselves, unable to see one another.

The call never developed the aesthetic qualities such as Blaauw (1896) and Hudson (1920) describe. However, Blaauw's description from captive birds of a four-note call is very close to those that I heard, while Hudson's five or six note calls are longer than any I experienced. It may be that in captivity with the female or females near at hand, the longer calls of the males are not necessary and can be abbreviated. Since I am fairly certain that the introductory note is aggressive in

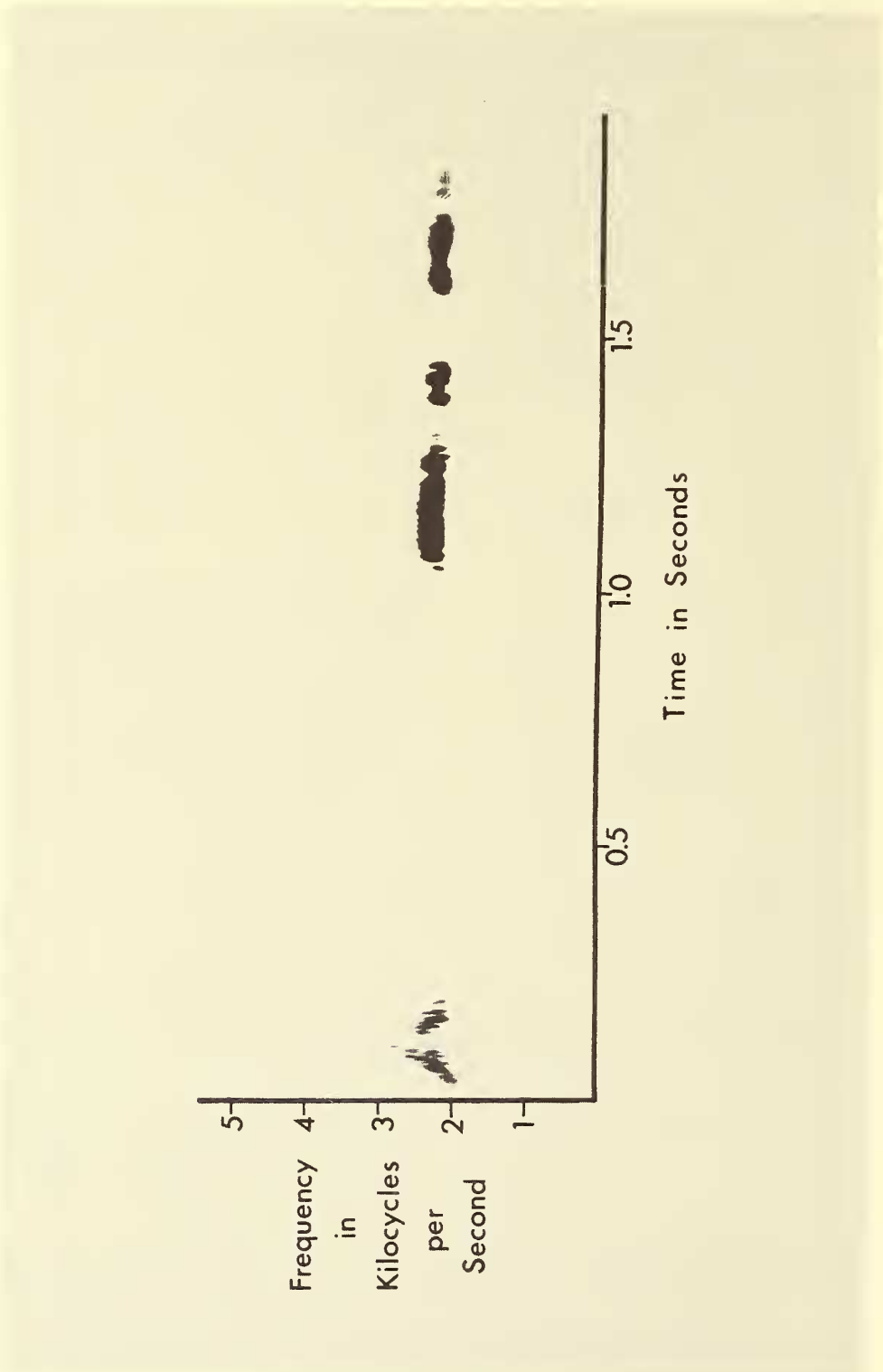

FIGURE 5. Audiospectrograph of the call of *Rhynchotus rufescens*.

function, it is tempting to speculate that the remaining notes in the call may function in stimulating and attracting females. An audiospectrogram of a typical call is seen in figure 5.

As mentioned earlier, their calling bouts probably take the place of physical aggressive encounters between males. It is rare for one male to be in sight of another bird when calling. In the wild these bouts probably keep males from actually meeting. In the aviary only one male at a time would perform calling bouts. Several days would elapse before another male might start bouts of calls. The reason for this, I feel, was due to the limited space. Given a larger area or areas farther separated, I am sure that more than one male would call at the same time as they do in the wild (Hudson, 1920).

Calling bouts lasted up to three hours but the average was slightly less than two hours. On the average, calls were repeated close to once per minute. The variations in call intervals were from about six minutes down to 20 seconds.

These bouts would occur during the breeding season on sunny days especially between 10 a.m. and 4 p.m. I did not notice any tendency toward calling at sunset as Hudson (1920) reports from the field.

Both males and females call and the calls are variable enough between birds so one can easily identify the individual.

When cornered, caught, held in the hand, and escaping after being released, *Rhynchotus* give an alarm or desperation cry. This is a repetitive, plaintive, short, ascending whistle. Individuals vary in the degree to which they must be pressed before giving this vocalization.

Males, especially, give a twittering call in what appear to be ambivalent agonistic situations but they usually have their crests raised. Often the twittering is followed by a growl. This growling vocalization is aggressive and like twittering is only used at very close quarters. A bird toward which a growling individual is oriented usually starts moving away. Many of the escape jumps of females were preceded by a male orienting on them, twittering, crest raising, slightly head bobbing, and then growling.

The males have only a very wavering, descending whistle which attracts the young. The young birds have a soft, screechy cry which seems to attract the male.

Discussion

Breeding season

The *Rhynchotus rufescens* specimens used in this study came from approximately 24° South latitude in Brazil. While working in the field, Laubmann (1930) obtained chicks in September; Holt (1928) saw eggs in early November; and Wetmore (1926), also in November, collected a female containing well-developed eggs; and Naumburg (1930) found fresh eggs in December. In the wild, then the breeding season appears to cover at least the four months of September through December.

In captivity at about 42° North latitude, these birds have shifted their breeding cycle by six months. Egg laying begins in earnest in March and is mostly over by the end of July.

Tinamou eggs

Yet to be answered is the question as to why tinamous, all of which nest on the ground, should lay eggs of such peculiar colors, shades, and gloss. Aposematic coloration can be ruled out, for the eggs are readily eaten by a variety of predators including man. No type of mimicry is known to be involved. Assuming that most of the egg predators are colorblind, one is still left with the aspects of shade and gloss.

A mirrored surface of an ovoid shaped object could have some cryptic quality in that it would reflect something of its environment. When such an object is on the ground, however, it reflects the brightness of the sky and thus is visually distinct from the darker substrate. In the aviary the tinamous would occasionally lay an egg without any gloss, perhaps indicating this trait could drop out easily with altered selection pressure. However, *Rhynchotus rufescens* usually ate their eggs of this type within a short time.

Eggs of darker shades would seem adaptive to those species nesting beneath the canopied rainforest. Yet many tinamous in this habitat lay light shaded eggs that would stand out even if not highly glossed. *Nothura maculosa* of the open, short grasslands might be expected to have lighter shaded eggs but they are of such a dark brownish-purple as to be almost black.

The conspicuousness of tinamou eggs, then, is probably being maintained because of some releaser function for the birds. They seem to be more of a signal than would be necessary solely to elicit male incubation. Perhaps a part of the function of the visual aspects of these eggs is to help call attention to the several females as to the nest's location. The sight of the egg(s) might stimulate ovulation and promote synchronous laying.

There are some species, however, in which only one female contributes to the clutch. And since these clutches are usually small, the egg would seem to be of little value in indicating the nest's location, the site with which the sole female would be familiar.

Also it was noted that in the aviary, *Rhynchotus rufescens* females were reluctant to go to the nest without the male. This would seem to insure that the females would get to the right location without the conspicuous eggs.

There are several adaptations which help mini-

mize the exposure of tinamou eggs which further indicates that they have no anti-predator qualities: (1) Several females (n = number of females) can produce a given clutch of eggs in 1/n the time of a single female. (2) If some of the females lay synchronously, this can further shorten clutch production time, and lessen traffic time to and from the nest. (3) Males may incubate for long periods without interruption, up to 38 hours in one species (Lancaster, 1964) and 46 hours in another (Lancaster, 1964b). (4) Males may sit very tight without being flushed, as Bump and Bump (1969) report stepping on an incubating *Nothura maculosa*. (5) Males may cover the eggs when leaving the nest as noted earlier in *Rhynchotus rufescens*, *Crypturellus noctivagus*, and *Eudromia elegans*. G. Bourne (pers. comm.) has seen the results of nest covering in *Crypturellus soui* and Lancaster (1964, and 1964b) saw this in *Crypturellus boucardi* and *Nothoprocta cinerascens*. Both observers stated, however, that covering was not complete. Bump and Bump (1969) mention this behavior in *Nothura maculosa* without saying how effectively the eggs were covered. I found this species to be quite ineffective.

Courtship feeding

In tinamous, birds with transient pair bonds, few and simple pair bond maintenance behaviors would be expected. In *Rhynchotus rufescens*, this is mostly limited to feeding and roosting together for short periods. Once, however, I saw a male pick up a small, light colored stone, mandibulate it, and then drop it. A female feeding next to him then did the same. The birds continued alternately at this behavior until the transfer had been made four times; the entire sequence lasted less than 30 seconds. Also, a few times I saw the female take food from the male's bill, a feat she could perform only when the male hesitated with food and she was feeding very close to him. The feeding side by side was not uncommon, but it was unusual for a bird to hesitate with a food item in its bill.

In *Crypturellus noctivagus*, it was much more common to see a pair dabbling with non-food items, such as a small stick 8 to 14 cm long. The male would pick up the stick and loudly mandibulate it. A nearby female usually approached and the male would drop the stick. The female would then pick it up and do the same as the male had done. This stick dabbling could go on as long as a minute, alternately between the male and female.

G. Bourne (pers. comm.) noted that vocalizations and uncovering of food by the female preceded copulation in *Crypturellus soui*.

Stokes and Williams (1971) have discussed similar behaviors which are common in gallinaceous birds.

Rump-up posture

Rump-up posture has been seen in several tinamous with interesting variations. In *Crypturellus* species, this posture is remarkably similar to that performed by the king rail, *Rallus elegans* (Meanley, 1957).

In *Crypturellus obsoletus*, this posture which displays the crissum is used to make the bird more cryptic. Seth-Smith (1904) describes and pictures the same posture in *Crypturellus tataupa*. The function again is to render the bird cryptic. In *Crypturellus noctivagus* it is cryptic but also is used in aggressive approaches. Beebe (1925) describes and illustrates a female courtship display in *Crypturellus variegatus* involving the rump-up posture. Lancaster (1964a) reports it as cryptic behavior of *Crypturellus boucardi* and reports it as occurring in *Tinamus major*.

In *Nothoprocta ornata*, the courtship display of the male involves a much less pronounced tilting forward, but the effect is enhanced by holding the folded primaries together tip-to-tip over the back. And in *Rhynchotus*, the aggressive posture is much less extreme than that seen in the *Crypturellus* species.

Tameness

I was struck by the variation in the degree of tameness of the tinamou species in captivity. *Rhynchotus* was quite wild at first but quieted down fairly rapidly. *Crypturellus noctivagus* was instantly tame, never taking to flight when approached. The *Nothura maculosa* never seemed very tame and never changed, a fact that was also noted by Bump and Bump (1969). All these birds were wild-caught. Welty (1963) discusses similar differences in other groups of birds.

Copulatory behavior

The copulatory behavior of tinamous is intriguing with each species so far having its own unique variations. This will be a valuable source of taxonomic and evolutionary information when more species have been studied.

The problems of large birds orienting properly during copulation have been noticed by W. Schleidt (pers. comm.), especially in the turkey (*Meleagris gallopavo*), and his proposing the turkey's "beard" to aid in this orientation has a definite parallel in *Rhynchotus*. The head of the female *Rhynchotus rufescens* touches the male's breast at about the same point where the "beard" is attached to the male turkey.

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